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CHAPTER FOUR

Towards an Integration of Biodiversity–Ecosystem Functioning and Food Web Theory to Evaluate Relationships between Multiple Ecosystem Services

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Abstract

Ecosystem responses to changes in species diversity are often studied individually. However, changes in species diversity can simultaneously influence multiple interdependent ecosystem functions. Therefore, an important challenge is to determine when and how changes in species diversity that influence one function will also drive changes in other functions. By providing the underlying structure of species interactions, ecological networks can quantify connections between biodiversity and multiple ecosystem functions. Here, we review parallels in the conceptual development of biodiversity–ecosystem functioning (BEF) and food web theory (FWT) research. Subsequently, we evaluate three common principles that unite these two research areas by explaining the patterns, concentrations, and direction of the flux of nutrients and energy through the species in diverse interaction webs. We give examples of combined BEF–FWT approaches that can be used to identify vulnerable species and habitats and to evaluate links that drive trade-offs between multiple ecosystems functions. These combined approaches reflect promising trends towards better management of biodiversity in landscapes that provide essential ecosystem services supporting human well-being.

1. INTRODUCTION

Ecologists have long been fascinated by the diversity of species and the complexity of species interactions (Darwin, 1859; Elton, 1927). Today, we use the term biodiversity to describe and compare variation among taxa at multiple levels of ecological organization: between and within populations, species, phylogenies, functional groups, trophic levels, food web compartments, and even habitat patches that explain landscape diversity. Concern over the consequences of global changes in all levels of biodiversity has motivated examination of the relationship between biodiversity and ecosystem functioning (BEF; Naeem et al., 2012). BEF combines community and ecosystem ecology to examine how changes in diversity affect a broad suite of ecosystem functions (EFs) (Hooper et al., 2005) and the services ecosystems provide to humans (ESs) (Costanza et al., 1997, MEA, 2005). More than three decades of BEF experiments have demonstrated that changes in diversity within each level of organization can influence several focal EFs as well as ecosystem services (ESs) that influence human well-being (Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2005; Tilman et al., 2014).

Increasingly, we are realizing that changes in biodiversity can simultaneously influence multiple interdependent EFs and associated ESs, such as pollination, pest suppression, and carbon sequestration (Cardinale et al., 2012; Gamfeldt et al., 2013; Raudsepp-Hearne et al., 2010). Yet, we lack mechanistic understanding of how multiple EFs are connected to losses or gains of biodiversity that can simultaneously occur across several levels of ecological organization (Wardle et al., 2011). By explicitly providing the underlying network of species interactions, food web theory (FWT) can make these critical connections. At least five perspective papers published in the last decade have suggested that an explicit food web perspective is an important conceptual contribution to the understanding of BEF relationships (Duffy et al., 2007; Ives et al., 2005; Rooney and McCann, 2012; Thebault and Loreau, 2006; Thompson et al., 2012). These papers have emphasized that both horizontal diversity (within trophic level) and vertical diversity (between trophic levels) can influence focal EFs, such as production of biomass and resource depletion (Cardinale et al., 2006; Thebault and Loreau, 2006). Here, we extend this rationale and discuss how merging BEF and FWT approaches would also contribute to the understanding of the trade-offs and mechanisms driving relationships between biodiversity and multiple EFs, as well as the services ecosystems provide to humans. In the sections that follow, we describe our perspective on the development, convergence, and limitations of BEF and FWT (Section 2). Next we discuss three principles that unite the two research areas, generating testable hypotheses that can be used to evaluate relationships between biodiversity and multiple EFs (Section 3). While increasing biodiversity may increase ecosystem functioning (i.e. grassland community production), it may limit the contribution of focal species to some ESs (i.e. production of grain for food) that benefit humans. Therefore, we close by considering how development of combined BEF–FWT perspective has contributed to better management of multiple ESs (Section 4).

2. CONTRIBUTIONS AND LIMITATIONS OF BEF AND FWT

The development and convergence of BEF and FWT have proceeded through three conceptual phases (Fig. 1). While not intending to present a comprehensive review of all research in both sub-disciplines, these phases provide a road map outlining the parallel and convergent concepts developed in both research areas. The first phase describes research that, for the most part, has been completed. The second phase describes research that currently is being pursued, while the third phase describes a promising line of

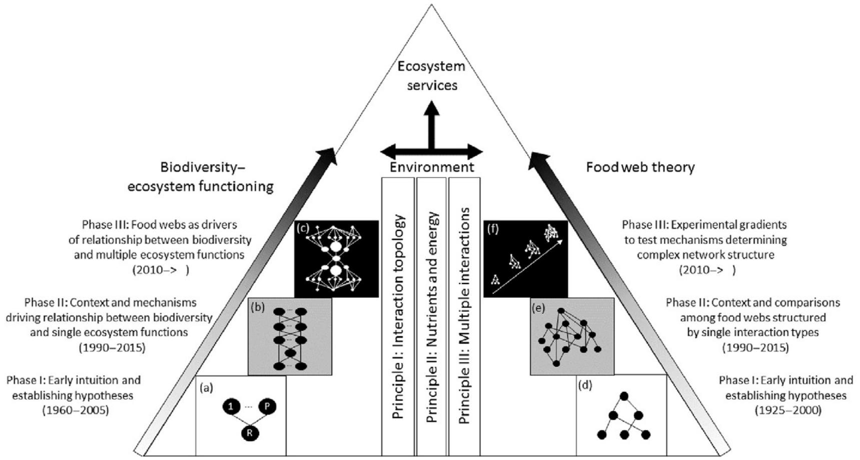

Figure 1 The models of biodiversity–ecosystem functioning (BEF) and food web theory (FWT) both utilize assumptions grounded in species interactions and flux of nutrients and energy. Three conceptual phases of research describe the development and convergence of these disciplines, which are united by three common principles allowing for the establishment of an integrative BEF–FWT framework (see text for description). Management of ecosystems providing multiple ecosystem services will benefit from an integrative approach that explicitly connects ecosystem functions and services to the network of species interactions that influence them.

inquiry that is still in its infancy. Assessment of these conceptual phases will allow us to consider how progress in the study of biodiversity, food webs, and ecosystem functioning may, or may not, be useful for management of species that provide essential ESs that benefit humans.

2.1 BEF and Species Interactions Concepts

2.1.1 First Phase BEF: Early Intuition and Establishing Hypotheses

As a research area, BEF is based on the intuition that ecosystems harbouring many species function differently than ecosystems with only few species. Experimental evidence for this intuition was lacking until initial experiments in agricultural (De Wit and Van Den Bergh, 1965) and natural grasslands (Berendse, 1983) demonstrated that plots with mixed plant species produced more biomass than monocultures of the same species (Hector et al., 1999; Roscher et al., 2004; Tilman, 1996). Disagreement surrounded the extent to which different experimental designs could test for mechanisms driving BEF relationships (Huston, 1997). Nonetheless, three hypotheses were proposed to explain increases in functioning resulting from higher diversity within a single trophic level: (1) complementarity effects, (2) sampling effects, and (3) selection effects. *Complementarity effects* evoke niche-based mechanisms to explain why unique attributes of each species reduce competition (Loreau and Hector, 2001) or facilitate associated species performances (Mulder et al., 2001) to enhance overall resource capture and use in mixed species communities. *Sampling effects* occur when a particularly effective species is more likely to be present in a more diverse community (Wardle, 1999). Sometimes considered in a similar category as sampling effects, *selection effects* transpire when the most effective species in monoculture also dominate ecosystem functioning in diverse communities, or reciprocally the most vulnerable species are diluted in diverse communities (Loreau and Hector, 2001). Because of the focus on plant diversity, each of these mechanisms focused on interactions within a trophic level, such as competition or facilitation, as the primary driver of ecosystem functioning. These hypotheses lead to a conceptual topology where species (i.e. producers (1-P in Fig. 1A)) are linked to a resource (R), and ecosystem functioning reflects the community's production of biomass or depletion of the resource (Fig. 1A). They also established an important initial paradigm shift in the understanding of biodiversity. That is, beyond being a response to environmental conditions, biodiversity now was also considered as a potential driver of ecosystem functioning (Schulze and Mooney, 1993).

Similar ideas regarding the influence of diversity on particular EFs were developed in multi-trophic systems, especially in the context of predator diversity effects on prey suppression in biocontrol (Pimentel, 1961). Emphasis was placed on discovery and naming of particular interaction pathways describing how consumers responded to, or caused, changes in plant diversity. For example, the terms 'associational resistance' and 'associational susceptibility' were coined and used to describe the indirect interaction by which the traits of neighbouring plants in more diverse communities do (Root, 1973) or do not (Atsatt and O'Dowd, 1976) influence the impact of herbivores on focal plants. Attention was focused on finding plant traits that served as underlying mechanisms behind associational resistance and associational susceptibility (reviewed in Barbosa et al., 2009). These included differences in plant chemistry (Karban and Maron, 2002), apparency (Perrin and Phillips, 1978), vegetation structure (Rauscher, 1981), and ability to attract predators (Dicke, 1994). Multi-trophic BEF research was not limited to plants and their interactions with aboveground consumers (Bardgett et al., 1999; Zak et al., 2003). Microbial-driven processes in soils were found to influence aboveground plant diversity and production by altering organic matter decomposition, developing mutualistic mycorrhizae–plant interactions, and modifying plant susceptibility to pathogens (Barbosa and Krischik, 1991; van der Heijden et al., 1998; Wolters et al., 2000). Despite the discovery of multiple potential interaction pathways, however, identifying general rules or predicting the effects of combinations of consumer species on EF proved to be difficult, especially in soil systems where soil fauna were highly omnivorous and played multiple ecological roles (Mikola and Setälä, 1998b). Therefore, although strong connections between aboveground and belowground consumers were established (De Deyn and Van der Putten, 2005), the context dependency behind the consumer–BEF relationships were not yet clear.

In the first phase of BEF research, the foundation was laid for examining the relationship between BEF in multi-trophic aboveground–belowground communities, and consumers were considered as both a response to, and a driver of, ecosystem functioning (Naeem et al., 1994). Species richness was indirectly (Tilman and Downing, 1994) and directly (Naeem and Li, 1997) manipulated, and debate focused on whether conclusions were biased by inferences drawn from particular experimental designs (Huston, 1997). This phase ended with a consensus statement that regardless of experimental design many, but not all, studies demonstrated an asymptotic relationship between biodiversity and ecosystem functioning such that functioning declined rapidly when species were lost from communities with low diversity (Hooper et al., 2005). The potential conservation applications and scale at which each mechanism operated, however, remained unresolved during this phase, particularly with respect to the influence of consumer diversity (Srivastava and Vellend, 2005).

2.1.2 Second Phase BEF: Context and Mechanisms Driving Relationship between Biodiversity and Single EFs

The second phase of BEF research moved beyond debates about experimental design and generated an explosion of studies used to evaluate the generality and context dependency of the relationship between biodiversity and ecosystem functioning (Cardinale et al., 2011). The type of diversity manipulated was considered as an important context for the influence of biodiversity on EF. For plants, not only species richness but also diversity at multiple levels of ecological organization, such as intra-specific genetic diversity, phylogenetic diversity, and functional trait diversity was also found to influence plant community production (Cadotte et al., 2008; Crutsinger et al., 2006; Flynn et al., 2011). In addition to grassland plants, the diversity of other groups of species, including consumers (Duffy, 2002), that range in body size from unicellular microbial systems (Bell et al., 2005) to trees (Rivest et al., 2015) was manipulated. Following up on the work of Mikola and Setälä (1998b), diversity of herbivores (Deraison et al., 2015; Duffy et al., 2003; Norberg, 2000), detritivores (Cardinale et al., 2002; Dangles et al., 2002), or predators (Cardinale et al., 2003; Finke and Denno, 2005; Straub and Snyder, 2006) were manipulated and ecosystem functioning was assessed by measuring depletion of resources in adjacent trophic levels. Ives et al. (2005) used basic Lotka–Volterra equations to identify a common vocabulary and conclusions between studies examining multitrophic and BEF interactions. Consumer diversity effects proved strong enough to cascade across multiple trophic levels in terrestrial (Wardle et al., 2005) and aquatic systems (Mancinelli and Mulder, 2015; Worm et al., 2003; but see O'Connor and Bruno, 2009), demonstrating that diversity effects on EF are not necessarily dependent upon study system or trophic level (Griffin et al., 2013).

The sensitivity of the response variables was considered as an additional factor that would influence BEF relationships, and the types of responses measured were expanded and compared (Allan et al., 2013; Balvanera et al., 2006; Hector and Bagchi, 2007). Ecosystem responses included soil nutrient cycling, decomposition, plant production, and soil water content, among others. Often not explicitly tied to ecosystem functioning, response of consumer community composition was assessed using several metrics including consumer species richness (Haddad et al., 2011), functional diversity (Best et al., 2014; Rzanny and Voigt, 2012), and consumer phylogenetic diversity (Lind et al., 2015). Consumers were found to be sensitive to manipulations of several types of plant diversity including plant species diversity (Haddad et al., 2009; Scherber et al., 2010), functional diversity (Symstad et al., 2000), and genetic diversity (Crutsinger et al., 2006). Their sensitivity to changes in plant diversity, however, was found to attenuate across trophic levels, with strongest effects of plant diversity on plant production and the abundance of their direct consumers, and diminished effects on higher trophic levels such as predators and omnivores (Haddad et al., 2009; Scherber et al., 2010). Considering these results together with studies manipulating consumer diversity, population dynamic models were used to demonstrate that bottom-up influences of plant diversity, and top-down influences of consumer diversity could interactively modify the relationship between biodiversity and focal EFs (Thebault and Loreau, 2003). This was confirmed by pioneering experimental tests, conducted predominantly in aquatic systems, which simultaneously manipulated diversity at multiple trophic levels (Bruno et al., 2008; Douglass et al., 2008; Fox, 2004; Gamfeldt et al., 2005; Jabiol et al., 2013).

Environmental conditions also were considered as a source of qualitative and quantitative variation BEF relationships. For example, plant diversity effects on ecosystem functioning were measured in experimental manipulations that simulated different global environmental change scenarios (Adair et al., 2009; Reich et al., 2001). The effects of biodiversity on ecosystem functioning were compared across different environmental contexts such as terrestrial, freshwater, and marine ecosystems (Cardinale et al., 2006; Covich et al., 2004), as well as primary producer or detritus-based ecosystems (Srivastava et al., 2009). In summary, this phase of research generated a wealth of case studies, which expanded the range of scenarios that could potentially influence BEF relationships.

To evaluate factors that influence magnitude and consistency of biodiversity effects on ecosystem functioning in this diverse array of experiments is a daunting task and this phase of research is currently in a period of synthesis (Cardinale et al., 2006). Meta-analyses generally support predicted biodiversity relationships for response variables such as plant productivity that are reported broadly across many experiments (Cardinale et al., 2012; Gamfeldt et al., 2015). Indeed, the influence of changes in diversity on plant production and decomposition can even surpass the magnitudes of impact imposed by other environmental change drivers such as climate warming, acidification, and nutrient pollution (Hooper et al., 2012; Tilman et al., 2012). However, when detailed responses are reported within single experiments, the influence of biodiversity on the magnitude and direction of effects have not proven as consistent (Allan et al., 2013). In a German grassland study, for example, plant diversity had positive effects on aboveground herbivore abundance, but no effect on belowground herbivore abundance (Allan et al., 2013). While this second phase of research answered questions about the strength and consistency of biodiversity effects across different environmental contexts, it also led to new inquiries as to how biodiversity affects connections between multiple EFs within a particular compartment (e.g. above- and belowground processes).

2.1.3 Third Phase BEF: Linking Multiple Functions and Scaling of Mechanisms

We are approaching a conceptual shift in BEF research. The variation in responses within experiments seen in the second phase demands an examination of how species influence connections between EFs. As with the conceptual shift in the first phase of BEF research, which established hypotheses explaining how biodiversity may not only be a response to environmental conditions but also a driver of EFs (Hillebrand and Matthiessen, 2009), we are generating new hypotheses about the influence of complexity in BEF (see Table 1 and Section 3). Now, rather than consumer species acting either as an additional response variable or as a driver of single functions, interactions between species may connect multiple EFs. This phase of research will seek a stronger understanding of connections between multiple response variables within a particular system (Bradford et al., 2014; Wagg et al., 2014).

Several quantitative approaches have been proposed to assess the simultaneous responses of multiple EFs (Byrnes et al., 2014; Lefcheck et al., 2015). These approaches examine correlations between functions, using data reduction approaches to generate multifunctionality metrics. Such metrics then can be compared across global data sets to assess whether results reflect generalizable insights about the relationship between biodiversity and ecosystem multifunctionality. For example, in a survey of 224 dryland ecosystems, 14 ecosystem responses were reduced into a single index of ecosystem multifunctionality, and increases in that multifunctionality index were associated with cooler temperatures and lower soil sand content (Maestre et al., 2012). Soil fauna and changes in net primary production by plants respond sensitively to desiccation in warmer drier soils, and they were implicated as possible drivers of ecosystem multifunctionality (Maestre et al., 2012). However, those responses were not reported directly in this study, illustrating that mechanisms behind multivariate responses sometimes can remain speculative in statistical analyses that involve dimensional reduction. Another approach is to embrace the complexity of consumer responses developed in phase two studies and consider connections between EFs as a component of complex food webs.

The groundwork for considering complexity-based approaches in BEF is built upon the observation that generalist predators and plants connect aboveground and belowground communities (Hooper et al., 2000; Scheu, 2001; Wardle et al., 2004). Beyond building a more complicated model, discovery of links connecting aboveground and belowground webs has emphasized that changes in species density and diversity in one food web compartment can alter the ecosystem functioning and services provided by species in another compartment (Bardgett and Van der Putten, 2014). Evaluations following this line of reasoning will benefit from quantitative methods typically used in FWT including, but not limited to, qualitative

Table 1 Three Common Principles Unite Biodiversity–Ecosystem Function (BEF) and Food Web Theory (FWT)

Principle	BEF	FWT	Hypotheses from Combined BEF–FWT	Methods	Application to Management of Multiple ES
I: Interactions occur between taxonomic units according to a topology	Unique aspect of each species allows coexistence and enhances resource capture of diverse communities using common resources (Complementarity effects)	Modular patterns of species interactions stabilize complex food webs (Compartmentalization effects)	CH1. Unique aspects of species within and between modules determine trade-offs and synergies in multiple ecosystem functions	Group detection (Gauzens et al., 2015)	Focus management on key modules within food webs to stabilize multiple ES. Prioritize conservation of key modules in space (Macfadyen et al., 2011; Montoya et al., 2015), or critical species connecting energy channels (Garay-Narváez et al., 2014; Terborgh et al., 2001)
II: Estimating fluxes of energy and materials through food web topology provides a common currency for assessing influence of biodiversity on ecosystem functioning	Diverse communities are more likely to include a species that enhances ecosystem functioning (Sampling effects)	Balances in transfer of biomass between trophic groups stabilizes food webs (Trophic effects)	CH2. Changes in diversity that limit uptake and transfer of biomass between trophic groups will influence multiple ecosystem functions	Ecosystem Network Analysis (Borrett and Lau, 2014)	Make management decisions based on the flux of energy through diverse food webs to stabilize multiple ES. Manage land-use intensity (Barnes et al., 2014), or harvesting of particular species (Fung et al., 2015) to enhance overall functionality

Continued

Table 1 Three Common Principles Unite Biodiversity–Ecosystem Function (BEF) and Food Web Theory (FWT)—cont'd

Principle	BEF	FWT	Hypotheses from Combined BEF–FWT	Methods	Application to Management of Multiple ES
III: Multiple types of species interactions influence ecosystem functioning	Dominance of species with traits that contribute positively to ecosystem functioning increases ecosystem functioning in diverse mixtures (Selection effects)	Balance of strong, weak, positive, and negative interactions stabilizes food webs (Interaction effects)	CH3. Trade-offs between multiple ecosystem functions are caused by dominance of species that have net positive species interactions with respect to one function but net negative interactions with respect to another function	Third-generation SEM (Grace et al., 2012)	Manage species interaction to enhance multiple ES. Prioritize timing of management actions based on its influence on direct and indirect interactions (Whalen et al., 2013) or prioritize conservation of multiple interactions themselves (Mougi and Kondoh, 2012)

Combined hypotheses (CH) result from development of a combined BEF–FWT perspective. These hypotheses are non-mutually exclusive, and here we highlight a few combinations that are well suited to test using quantitative methods developed using graph theoretic and systems theory. Results from these tests can be applied to ecological management strategies with the goal of enhancing and stabilizing multiple ecosystem services (ESs).

and quantitative descriptors of food web matrices (Bersier et al., 2002), group detection (Gauzens et al., 2015), ecosystem network analysis (Borrett and Lau, 2014; Ulanowicz, 2011), and third-generation structural equation modelling (SEM) (Grace et al., 2012). These tools can be used to characterize the structure and dynamics of whole ecosystems using an *interaction topology* to describe the *flux of nutrients and energy* through ecosystems. Although they place slightly different emphasis on the importance of structure and function, each tool establishes connections that mechanistically explain trade-offs and correlations between biodiversity and multiple EFs. Questions such as 'How often are species with positive effects on one function directly or indirectly connected to species that have negative influence on a second?' will be asked in this phase. Experiments here will reflect a convergence of BEF and FWT and test the relationship between the structure of complex food webs, biodiversity, and multiple EFs.

While we initially referred to the importance of above- and belowground compartments in the previous paragraph, similar relationships between food web structure and multiple EFs should exist in all ecosystems that are composed of discrete compartments. Traditionally, compartmentalized systems include aquatic ecosystems composed of benthic and pelagic compartments (Krause et al., 2003), coastal and riparian ecosystems composed of terrestrial and aquatic compartments (Polis and Hurd, 1996), agricultural fields composed of margins and croplands (Macfadyen et al., 2011), and any kind of ecosystem spanning environmental gradients that have thresholds in community interactions. This assortment of food web scaling allows us to think about how BEF relationships developed in small field plots may apply to changes in biodiversity at a landscape scale. This is an essential step to translate results from BEF experiments to broader scale management of ESs (Díaz et al., 2006; Kremen, 2005).

This third phase of BEF research, therefore, will move beyond evaluations of context-dependent effects to evaluate the influence of interactions among consumers in complex communities on multiple EFs (Fig. 1C). Consumers will be considered not only for their direct effects on resource uptake and production of biomass but also for their roles linking multiple EFs. The expectation is that the asymptotic relationship between BEF will be replaced by a non-saturating relationship when multiple EFs are considered, although trade-offs between some functions will limit the magnitude of this effect. To identify and evaluate such trade-offs, BEF will benefit from the conceptual advances being made in FWT, as described below. Network approaches will be used to test how relationships between changes in biodiversity and complex species interactions will influence ecosystem functioning and ES that influence human well-being.

2.1.4 Limitations of BEF with Respect to Understanding the Role of Consumers in Ecosystem Functioning

Much of the early debate about relationships between biodiversity and ecosystem functioning centred around the generality and strength of inferences that could be made regarding mechanisms revealed by particular experimental designs (Huston, 1997). Unfortunately, complex experimental designs have limited simultaneous manipulation of density (Griffin et al., 2008) and diversity at multiple trophic levels (but see experiments in aquatic systems emphasized above), which are necessary to evaluate the causal relationships between consumer community composition and ecosystem functioning. Complex experimental designs can also make it difficult to establish adequate replication needed to capture the shape of non-linear relationships between species–environment, species–species, and diversity–function relationships. Therefore, the classic BEF approach of manipulating diversity and measuring the response of ecosystem functioning has limitations that hinder the types of inferences made about the role of consumer as drivers of BEF relationships.

To overcome these limitations, experimental studies testing the influence of consumer diversity on EFs tend to take one of three approaches. First, some are conducted in simplified, but experimentally tractable meso- and micro-cosmos (O'Connor and Bruno, 2009; Setälä et al., 1998; Wardle et al., 2005). Second, others manipulate consumer diversity in more natural field settings without simultaneously manipulating plant diversity (Deraison et al., 2015; Schmitz, 2009). Such consumer diversity manipulations in field studies are often conducted in systems composed of monocultures of plants, such as agricultural fields (Snyder et al., 2006) or salt marshes (Finke and Denno, 2005), which makes it difficult to examine cause and effect relationships between drivers of plant and consumer diversity. The third alternative has been to manipulate consumer abundance using pesticides (Eisenhauer et al., 2011; Siemann and Weisser, 2004), which can be an effective way to control broad functional groups, but makes it difficult to determine the contribution of species diversity to responses, in part because biocides can have non-target effects (both direct and indirect) on other species. Despite the unique strengths and weaknesses of each of these three approaches, results frequently reveal unexpected indirect and non-trophic effects of consumers (Hawlena et al., 2012; Hines and

Gessner, 2012). For example, Losey and Denno (1998) found that predatory coccinellids hunting in plant canopies elicit a defence response in their aphid prey where the aphids drop to the ground causing them to be more susceptible to predation by ground-foraging carabids. Together, the combined impact of more diverse predator assemblages composed of coccinellids and carabids has a synergistic effect on pest suppression resulting from a change in prey behaviour that cannot be predicted by adding the direct consumption of the two predators alone (Losey and Denno, 1998). Consequently, theoretical approaches capable of modelling the outcome of multi-trophic interactions using complex effective competition matrices are difficult to parameterize from purely density-dependent approaches (Fowler, 2013).

Integrating more complex food web and network responses into studies that manipulate species diversity of a single trophic level may be a better direction because it allows quantification of multiple known interaction pathways and tests of when one can, or cannot, predict trade-offs or feedbacks among multiple EFs. However, in experimental studies, the limitations imposed by a lack of simultaneous manipulation of consumer communities remain. Furthermore, scaling of biodiversity effects inferred from small, short-term field plot experiments to assess the long-term stability of ecosystem functioning at landscape scales is a persistent challenge. Ultimately, pairing and comparing of multiple approaches including experimental manipulation of species abundance and diversity in the field, simulated extinctions, and dynamic food web models likely will provide the most robust understanding of biodiversity effects on multiple EFs.

2.2 FWT and Species Interactions Concepts

2.2.1 *First Phase FWT: Early Intuition and Establishing Hypotheses*

As a research area, the study of food webs is older than BEF, so we summarize a comparatively longer duration of inquiry in this first phase of research. Early FWT used graphic depictions of predator–prey interactions to illustrate the trophic pathways by which energy and biomass flow through ecosystems (Fig. 1D; Elton, 1927). These graphics generated hypotheses that there are emergent and generalizable properties of food web structure that allow populations and communities to be stable (Cohen, 1977; Pimm et al., 1991; Sugihara et al., 1989). Notably, there were strong conceptual divides between empiricists and theoreticians, as well as between those who preferred to study webs in terms of the natural history of species and those interested in physical and chemical attributes. Nonetheless, three main classes of hypotheses were suggested to influence the persistence and stability of food webs: (1) trophic structure effects, (2) interaction effects, and (3) compartmentalization effects. *Trophic structure effects* suggest that the amount of available biomass at a particular trophic level regulates food webs (Lindeman, 1942; Odum, 1969; Ulanowicz and Kemp, 1979). Debates focused on the importance of predation (top-down) as opposed to competition for resources (bottom-up) in stabilization of focal populations and communities at each trophic level (Hairston et al., 1960; Menge and Sutherland, 1987). The proportions of species in each trophic level also were thought to be scale invariant with respect to the number of species in the web (Cohen, 1977; but see Briand, 1983). *Interaction effects* occur when the number of interactions connecting species influence food web stability (MacArthur, 1955; Pimm, 1979). Addition of realistic patterns of interaction strengths revealed that highly connected species, such as generalists and omnivores, that have weak connections to many other species can stabilize food webs by relaxing predation pressure on populations at low densities, and allowing them to recover from disturbance (de Ruiter et al., 1995; Fagan, 1997; McCann et al., 1998). *Compartmentalization* effects transpire when sub-webs of species, often called modules, interact more with each other than with other species in the web. This clustering of interactions can limit the effects of disturbance to more localized modules within the food web (May, 1973; Yodzis, 1982). Compartmentalization effects can be limited by generalist species that link species in different modules, lending support to the idea that these effects may be weak in real systems (Pimm and Lawton, 1980). Some supporting evidence was found for each of these hypotheses, although the strength and consistency of effects with respect to the influence of changes in biodiversity on ecosystem functioning was not clear (Jones and Lawton, 1995; O'Neill, 2001).

As a field of expertise, FWT has placed less emphasis on consensus statements than BEF. The end of this phase was marked by a particularly insightful review by McCann (2000) that described the role of diversity–stability relationships in both BEF and FWT. With respect to FWT, McCann (2000) highlighted the influence of equilibrium dynamics on complexity–stability relationships as a key assumption that divided theoreticians and empiricists. Sadly, at around this time, the eminent ecologist Gary Polis died. Polis' work was providing the empirical evidence that was needed to challenge theoretical dogma suggesting that omnivory was rare and complex systems were unstable. He did so by quantifying the complexity and high degree of omnivory in desert food webs (Polis, 1991) and by documenting the strong influence of subsidies that cross traditionally subdivided landscape compartments (Polis et al., 1997). In time, reflection on his research reinforced the clear need for stronger integration of empirical and theoretical approaches in FWT.

2.2.2 Second Phase of FWT: Context and Comparisons among Food Webs Structured by Single Interaction Types

Inconsistencies between empirical and theoretical results led to an explosion of research testing the generality and context dependency of the relationship between food web structure and stability. The sensitivity food webs to disturbance was thought to depend upon how stability was defined and measured; there was an explosion of metrics used to describe network stability, including resilience, invasibility, persistence, permanence, coherence, and robustness (McCann, 2000; Pimm, 1984). Rather than being restricted to simple definitions of stable or unstable food webs a broader range of strategies leading to stability expanded our understanding of whole system dynamics in diverse food webs.

The generality and context dependency of each of the three main hypotheses also were tested. For example, debates focused on whether trophic effects were dependent upon study system, such as aquatic (Strong, 1992), aboveground (Shurin et al., 2006), and belowground (Mikola and Setälä, 1998a), or diversity of species within a trophic group (Hooper et al., 2005; Hunter and Price, 1992). The definition of interaction effects also was clarified to include and distinguish between trophic, indirect, and non-trophic interactions such as ecosystem engineering (Jones et al., 1994; Wootton, 1994). To determine the influence of different types of interactions on food web structure, traditional predator–prey interaction webs were compared with those structured by parasitism (Dunne et al., 2013; Lafferty et al., 2008) and mutualism (Bascompte and Jordano, 2007; Thebault and Fontaine, 2010). The existence and consequences of compartment effects also were debated among empiricist and theoreticians alike. In soil food webs, close interactions among species from different trophic levels were found to form compartments with divergent energetic pathways (Moore et al., 2005; Rooney et al., 2006). Some skepticism surrounded whether these effects reflected a general property of food webs because at least two lines of evidence suggested that sub-webs traditionally considered to be quite separate were found to be linked more closely than previously thought. Aquatic and terrestrial sub-webs were found to be linked by cross-habitat resource subsidies of plants (Nakano and Murakami, 2001; Polis et al., 1997) and animals (Dreyer et al., 2012).

Further, aboveground and belowground sub-webs were found to be linked by plants and generalist predators (Wardle, 2002). Previously, FWT focused on comparisons of aquatic, aboveground, or soil systems, and almost all BEF studies focus on either aquatic or terrestrial systems in isolation. Discovery of connections across compartments suggested that disturbances to any one part of the food web potentially could have much farther-reaching consequences than previously expected. Yet, development of suitable algorithms suggested that compartmentalization might be common in real food webs (Fortuna et al., 2010; Krause et al., 2003; Stouffer and Bascompte, 2011). Differences between studies demonstrating connections between compartments, and those demonstrating that compartmentalization was common reinforced interest in experimental studies examining causal drivers influencing the relationship between structure and function in food webs.

This second phase of FWT can be characterized by a strong emphasis on more finely and evenly resolved food webs, and comparisons between webs with different kinds of interactions (Fig. 1E; Ings et al., 2009). A growing number of food web databases facilitate sharing of food web data (Webs on the Web, ECOweB, Interaction Web Database-NCEAS) (Mulder, 2011). Outside of a limited set of examples, however, most assessments of food web structure are made from comparisons of detailed but unreplicated webs across ecosystems (Dunne et al., 2002). In contrast, considerably simplified food webs are the focus in replicated experiments (Denno et al., 2003; Menge et al., 2004). The increasing number of well-resolved food webs that are readily available in databases allows comparative tests of whether the consequences of disturbance can be generalized across all food webs, or if they differ for food webs in different environments.

2.2.3 Third Phase of FWT: Linking Multiple Interactions with Ecosystem Functioning

A key innovation in this phase of FWT research will be the use of experimental gradients to identify causal drivers of food web structure (Fig. 1F; Baiser et al., 2012; Thompson and Townsend, 2004; Tylianakis et al., 2007). FWT will benefit from BEF studies that use rigorous experimental designs to examine the relationship between biodiversity and ecosystem functioning. BEF experiments will also contribute detailed records of species diversity and nutrient fluxes to food web models that had previously focused on either species interactions or flux of nutrients through aggregated nodes. In this phase, therefore, consumer interactions will be considered not only for their direct effects on other consumers but also for their roles in providing and linking multiple EFs and services (i.e. pollination, pest suppression, and carbon sequestration).

The groundwork for this line of reasoning was built upon the realization that organismal growth and ecosystem dynamics are both constrained by the first principles of physics and chemistry (Brown et al., 2004). To show how species influence the flux of biomass through well-resolved food webs, network nodes in this phase will more commonly integrate traits such as mass and abundance (Cohen et al., 2009), metabolism (Barnes et al., 2014), or multivariate functional traits (Rzanny and Voigt, 2012; Rzanny et al., 2013). Stoichiometric traits (C:N:P) of plants and animals also could provide informative constraints of food web structure (Mulder et al., 2013; Ott et al., 2014). Predators and detritivores generally seem to have higher nutrient content than their prey (Martinson et al., 2008) and to maintain their body composition omnivores may supplement their low quality plant diets with higher nutrient prey (Denno and Fagan, 2003). Species with high nutrient content could be highly connected and central in the food web, effectively serving as keystone nodes that have a strong influence on both ecosystem functioning and food web stability. To our knowledge this expectation has not yet been tested in complex food webs. Notably, stoichiometry could turn out to be a key trait associated with complementarity effects in BEF research (Hillebrand et al., 2014). Therefore, metabolic theory and ecological stoichiometry theory, which describe the physiological and nutritional constraints of feeding interactions, provide important background for integrating BEF and complex interaction webs (Mulder and Elser, 2009; Mulder et al., 2013). These theories also permit explicit consideration of the scaling of interactions, from genes to individuals to ecosystems (Allen and Gillooly, 2009; Sterner and Elser, 2002). Consequently, it is likely that the traditional emphasis on aggregation of trophic groups will be relaxed in this phase. Instead, emphasis will be placed on the role of all levels of biodiversity in ecological networks that underlie the relationship between biodiversity and multiple EFs.

In summary, rather than relying entirely on comparative approaches to examine the consequences of different types of ecosystems (i.e. aquatic, aboveground, belowground) or interaction types (i.e. antagonistic vs. mutualistic or ecosystem engineering) on food web structure and stability, this phase of research will place a stronger emphasis on establishing causal drivers of changes in network structure and function. Relationships between complex ecological networks and ecosystem functioning will be evaluated by examining changes in the structure of species interaction webs across experimental gradients (Fig. 1F), by integrating species traits, and by including multiple interaction types into each web (Fontaine et al., 2011; Melian et al., 2009; Sanders et al., 2014; Suave et al., 2014). This phase of research, therefore, is likely to produce a better understanding of relationships between factors thought to influence food web structure (i.e. trophic effects, interaction effects, and compartmentalization effects) and factors associated with BEF relationships (complementarity effects, sampling effects, and selection effects). This understanding may help resolve long-standing debates about the relationship between interaction complexity, community stability and ecosystem functioning. As we look forward, we expect that this next phase of food web research will focus more strongly on scaling of multiple interaction types from local to global scales, and more directly link changes in network structure across all levels of ecological organization with the ability of ecosystems to maintain functions that provide services to human society.

2.2.4 Limitations of FWT with Respect to Understanding the Role of Food Webs in Ecosystem Functioning

The main limitation of FWT is that quantifying the influence of species interactions on ecosystem functioning remains deceptively difficult, due to challenges measuring the particular interaction (presence and strength), and subsequently establishing that the interaction is relevant for EF (Nowak, 2010). For example, some species-specific interactions, such as those among plants and pollinators (Burkle et al., 2013), or plants and some monophagous herbivores (Southwood and Leston, 1959), can be readily observed in the field and these interactions are, as a consequence, well established. However, documenting the presence of an interaction may not demonstrate its importance for ecosystem functioning. Feeding by an early-season herbivore may induce plant defences that increase resistance to herbivory later in the season (Faeth, 1986). In some cases, therefore, herbivory can enhance rather than limit plant productivity.

Feeding behaviour also may be cryptic, infrequent, and variable not only according to life stage (juveniles vs. adults) but also across seasons and years, making direct observations of many taxa challenging (Kaartinen and Roslin, 2012; Polis, 1991). Some chemical tracers, such as stable isotopes, lipid fatty acids, and molecular analysis of gut contents, can trace dominant energy channels and identify ingested prey to some degree of taxonomic resolution (Traugott et al., 2013). Even when sophisticated empirical methods are coupled with a quantification of prey availability, however, they may not reflect diet choice in other habitats where different prey species are available. Therefore, regardless of original method reporting the interaction, food webs based on potential interactions from the literature may not reflect realized feeding interactions in other habitats. For this reason, there is much interest in approaches that identify simple trait axes that can be used to distinguish the presence of a trophic interaction (Cohen and Newman, 1985; Eklöf et al., 2013; Williams and Martinez, 2000). Given the assumption that there are generalizable rules structuring food webs, machine learning systems can be used to detect patterns in webs and suggest where missing predator–prey links may be expected (Tamaddoni-Nezhad et al., 2013). Whether machine learning approaches can take the next step to accurately detect a full complement of positive and negative species interactions as well as their influence on ecosystem functioning remains an open question (Tamaddoni-Nezhad et al., 2015). Food webs developed using combined empirical and theoretical approaches constantly improve (and challenge) our understanding of food web structure.

Differences in sampling methods also may limit the application of the FWT to ecosystem functioning. Sampling methods, which may be important to assess the biology of each taxon, can make it difficult to assess density, biomass, and interaction strengths using common units of measurement for all taxa (Nowak, 2010). For example, pitfall traps (Birkhofer et al., 2008) and observations of flower visitation by pollinators (Ebeling et al., 2011) provide information on activity patterns rather than density or biomass *per se*. Conversely, the abundance of soil fauna sampled with soil cores (Kempson et al., 1963; MacFadyen, 1961) and aboveground fauna sampled with vacuum samplers (Brook et al., 2008) are more easily reported on a per unit area basis. Again, machine learning can be used to compare interactions gleaned from each approach (Tamaddoni-Nezhad et al., 2013). However, the per capita dry body mass of different soil faunal groups can range more than 10 orders of magnitude, from $<10^{-6}$ g for nematodes up to several grams for some earthworms (Sechi et al., 2015). Life history traits and foraging range can also vary by several orders of magnitude among species that coexist in the same habitat. Therefore, sampling that effectively captures the spatial distribution of each taxon at a scale that is comparable across taxa is challenging in many experimental plots where space is limited (De Deyn and Van der Putten, 2005; Kremen et al., 2007). Well-coordinated multi-investigator experiments that unite the efforts of scientists with a wide range of taxonomic and computational expertise (i.e. Roscher et al., 2004) have much to contribute to the further development of FWT.

3. PRINCIPLES FOR INTEGRATING BEF AND FWT

The models of BEF and FWT both describe species interactions and fluxes of nutrients and energy, and categorizing research as one approach or the other is not always a clear-cut distinction. For example, production of fish in aquatic habitats and pest suppression in terrestrial agriculture are two examples of particular ESs studied extensively using both approaches. Nevertheless, to understand when changes in biodiversity will directly, or indirectly, influence multiple ESs, it is useful to consider combined hypotheses (CH) that result from multiple possible groupings of hypotheses thought to explain diversity–functioning–stability relationships in BEF and FWT. Further, in this section we demonstrate that common quantitative frameworks can be established using three key principles that bridge assumptions behind both BEF and FWT. We acknowledge that none of these principles is new, but considered together in light of focal BEF and FWT hypotheses, they form a road map for hypotheses that guide the management of ESs essential for human well-being (Table 1).

3.1 Principle I: Interactions Occur between Taxonomic Units According to a Topology

Principle I may seem like a truism to ecologists in each area of expertise. Traditionally, however, the topologies of BEF and FWT interactions have been a bit different. The topologies of BEF studies often focus on species interactions within a single trophic level, or species that are connected by flux of nutrients and energy through simple interaction chains. The focus has been to describe taxa that coexist as competitors or facilitators feeding on the same resource (Fig. 1A and B). Complementarity effects, or unique aspects of each species, enhance an EF that reflects their resource consumption or collective accumulation of biomass (Table 1: Principle I-BEF). In contrast, because detailed diet information frequently is missing, food web studies often implicitly assume high levels of functional redundancy by aggregating species that share the same predators and the same prey into nodes that reflect 'trophic species' (Martinez, 1991; Williams and Martinez, 2000). The network topology is used to determine whether random or ordered loss of trophic species will trigger secondary extinctions. Therefore, trophic species generally are not directly associated with particular EFs (but see Gross and Cardinale, 2005). Instead, indexes describing the topology of species interactions (i.e. compartmentalization, connectivity, and omnivory) are associated with properties of food web stability, which are then indirectly associated with stability of ecosystem functioning as a whole, but without reference to particular functions (Table 1: Principle I-FWT).

Patterns of interactions among species will be an important predictor of when changes in species diversity that influence one focal EF will also affect other EFs (Table 1: CH1). Combined BEF–FWT approaches use group detection to consider the distribution of functionally redundant species within and between modules (Gauzens et al., 2015). Group detection in food webs can be applied to management of multiple ESs in several ways (Table 1). Detection of functionally unique compartments in space can be used to prioritize conservation of habitat patches that are particularly important for ESs or disservices. Such spatial compartments have been found in agricultural (Macfadyen et al., 2011) and salt marsh (Montoya et al., 2015) landscapes. Group detection also can identify particular species or resource inputs with high probability to influence multiple ESs. For example, a lot of attention has been placed on conservation of top predators that link energy channels due to their potential to drive 'ecological meltdowns' (Terborgh et al., 2001), and on regulation of pollutants and nutrients that causes dominance of one energy channel over another (Garay-Narváez et al., 2014; Scheffer et al., 2001).

3.2 Principle II: Energy and Material Fluxes through Food Webs Provide a Common Currency for Assessing the Influence of Biodiversity on Ecosystem Functioning

Principle II is important for understanding how biodiversity-mediated changes in the topology developed in Principle I contribute to ecosystem process rates. Combined BEF–FWT hypotheses propose that increases in biodiversity are not only more likely to include species that enhance ecosystem functioning within a trophic level (Principle II-BEF) but also more likely to include species that more efficiently transfer energy between trophic levels (Table 1: Principle II-FWT). This classic hypothesis of growth-defence trade-offs (Coley et al., 1985; Herms and Mattson, 1992) has rarely been considered in terms of flux of nutrients and energy in complex networks.

Combined BEF–FWT suggests that changes in diversity that limit uptake and transfer of biomass between trophic groups will influence multiple EFs (Table 1: CH2). Tests using dynamic equations (Carpenter et al., 1985; de Ruiter et al., 1995) or ecological network analysis (Borrett and Lau, 2014; Ulanowicz, 2011) can be used to examine how changes in biodiversity influence the stocks and flows of biomass, nutrients, and energy through food webs. Depending on the resource pool, these biodiversity induced changes in energy fluxes can be related to management of multiple ESs (Table 1). Robust management recommendations for land-use intensity rely on an understanding of ES trade-offs (Goldstein et al., 2012) that would benefit from an explicit BEF–FWT perspective. The conversion of land from rainforest to agricultural production of oil palm, for example, had strong effects on the efficiency of top predators, resulting in reductions in ecosystem functionality that were greater than effects of biodiversity loss alone (Barnes et al., 2014). Ecosystem network analysis that captures multi-trophic BEF relationships also can be used to prioritize conservation or harvesting of particular species. For example, production of fish in marine and freshwater systems is a focal ES that is well suited to combining BEF and trait-based food webs with quantitative links. A multi-trophic analysis from a large marine ecosystem demonstrated that selective harvesting of fish by body size, as opposed to unselective harvesting can change the biodiversity–ecosystem functioning relationship from unimodal to linear due to effects of releasing prey from larger predators (Fung et al., 2015). Such combined BEF–FWT evaluations give critical insights into when loss in functioning due to selective harvesting can overwhelm benefits gained from prey release (Fung et al., 2015). Consideration of how these trade-offs also influence multiple EFs will be important for developing an economic valuation of biodiversity.

3.3 Principle III: Multiple Types of Species Interactions Affect Ecosystem Functioning

Principle III states that multiple types of species interactions influence ecosystem functioning, including ecosystem engineering, parasitism, mutualism, and predation. This idea, which was presented in early models (May, 1972), and revisited recently (Mougi and Kondoh, 2012), serves as an important reminder about the diversity of interactions that influence food web structure. Principle II focuses on flux of nutrients and energy through the interaction topology. However, information is reported rarely about body size, and nutrient content for pathogens (Latz et al., 2012), parasites (Dunne et al., 2013), or pollinators (Woodward et al., 2005), despite the strong influence of these interactions on the maintenance of plant diversity (Klironomos, 2002), and BEF relationships (Maron et al., 2011; Schnitzer et al., 2011). To support principle III, therefore, we revisit the focal hypotheses of each research area. BEF research suggests that dominance of species with traits that contribute positively to ecosystem functioning selects for increased functioning in diverse mixtures (Table 1: Principle III BEF).

Combined BEF–FWT perspectives would then ask, 'Whose trait is it anyway?' by additionally considering the net effect of species interactions as an extended trait (Table 1: Principle III-FWT). A focal EF is then the net effect resulting from the sum of beneficial and antagonistic interactions described by network structure. Trade-offs between multiple EFs are caused by dominance of species that have net positive species interactions with respect to one function but net negative interactions with respect to another function (Table 1: CH3).

Third-generation SEM is well suited to evaluate CH3 (Grace et al., 2012). EFs can be conceptualized as latent variables that quantify the net effect of positive and negative interactions connected by an interaction topology (see Text Box 2 in Mulder et al., 2015). If data are collected in the same framework, SEM also stands to be a useful for comparing results from experimental manipulations with observational studies that examine relationships between consumer diversity and ecosystem functioning in natural ecosystems (Duffy et al., 2015; Mora et al., 2011). These results also could be used to manage multiple ESs (Table 1). Whalen et al. (2013) used SEM to examine associations between sea grass production and the direct and indirect effects of crustacean and gastropod mesograzers. They found temporal shifts in interactions among species that could be used to identify times where management actions such as nutrient regulation would be most effective. Here, additional information about multiple EFs and diverse species interactions would be particularly valuable. It has been suggested that interaction diversity itself should be a high conservation priority (Tylianakis et al., 2010; Memmott et al., 2007), as loss of multiple interaction types can have consequences for ecosystem functioning that precede loss of species diversity (Mougi and Kondoh, 2012; Valiente-Banuet et al., 2014). Establishing relationships between habitat conservation value and interaction networks would be needed to use this suggestion in practice (Heleno et al., 2012). Nonetheless, it is likely that more explicit consideration of species interactions as a source of complementarity effects that influences BEF (Eisenhauer, 2012; Poisot et al., 2013) and connects multiple EFs will improve decisions support for management of multiple ES.

4. CONSIDERING TRENDS IN BEF–FWT RESEARCH FOR BETTER MANAGEMENT OF MULTIPLE ESs

The concepts of ecosystem functioning and ecosystem services often use similar terminology and reasoning (Birkhofer et al., 2015; Mace et al., 2012; Mulder et al., 2015; Reyers et al., 2012). For example, results from soil food web studies that focus on mineralization, assimilation, and feeding rates to estimate energy fluxes (Moore and De Ruiter, 2012) can be used to assess ESs related to carbon sequestration (De Vries et al., 2013). In Section 3, we provided targeted examples demonstrating applications of combined BEF–FWT approaches. Here, we more broadly consider long-term trends in BEF–FWT research (see Section 2) as they apply to management of multiple ESs.

BEF and FWT research trends have led towards increased mechanistic understanding of detailed interaction webs (Fig. 1). However, outside of experimental settings detailed information about species interactions and ecosystem process rates often does not exist. It is tempting to say that the studies describing the complexity of species interactions reflect research mired in detail that cannot be applied to management of ESs. However, a potential difference between BEF and ES research suggests that detailed perspectives will prove to be useful. BEF research primarily focuses on how biodiversity influences functioning of communities (i.e. all dark green squares (black in the print version) species in Fig. 2), whereas ES allows for prioritization by stakeholders who may place differential value on particular services provided by separate species within the community (i.e. crop species indicated with a star) species in Fig. 2; Luck et al., 2009). Therefore, identifying and key trade-offs in BEF–FWT will provide important information for valuation of the ecological consequences

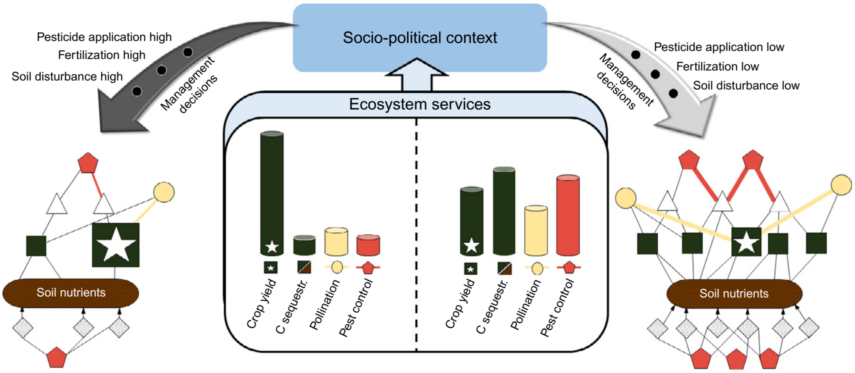

Figure 2 A unified BEF and FWT framework for management of multiple ecosystem services. This cartoon depicts connections between the diversity of species in a food webs and the management of multiple ecosystem services. Management decisions that focus purely on one ecosystem service such as crop yield can limit the balance of ecosystem services provided by other species in complex food webs (triangles-herbivores; pentagons-predators, circles-pollinators; diamonds-soil fauna). Socio-political context related to human population density, and stakeholder interests can influence feedbacks between ecosystem services and management of complex ecosystems.

ES trade-offs (i.e. Fig. 2 crop yield and C sequestration; De Groot et al., 2012; Gamfeldt et al., 2013; Lester et al., 2013).

While BEF focuses more on causal relationships between species in small-scale field plots, the focus of much ES research is on correlative patterns, often between land-use and ES, at larger spatial scales (Raudsepp-Hearne et al., 2010; Seppelt et al., 2011). Here, BEF–FWT research trends towards identifying causal drivers of thresholds in food web compartments could be useful for policy. Identifying factors that influence the connection between aboveground–belowground and terrestrial–aquatic networks is especially relevant because provenance of management agencies traditionally has been divided by food web compartment, trophic level, or ecosystem type. In the past policy for soil management was determined by different agencies than for air quality, and similarly policy for agricultural systems was made by separate governmental agencies than for ocean fisheries. Following trends in BEF–FWT research in recent decades, key agencies determining environmental policy, such as the US Environmental Protection Agency, DEFRA, the European Commission, and the Environmental Ministries of nations like Germany, have reorganized their policy-research programmes to reflect a more general consideration of ecosystem dynamics (TEEB, 2008; EPA, 2008). This is good news for those who propose to use biodiversity to manage the flux of nutrients across landscapes (Cardinale, 2011; Diaz and Rosenberg, 2008) and suggests that trends towards understanding BEF–FWT relationships across spatial scales should lead to more integrated ES policy.

Trends towards combined BEF–FWT research increasingly rely on quantitative network approaches. The challenges of modelling non-linear responses, feedbacks, and multiple interaction types in complex systems also apply to management of ES, which additionally considers the coupling of ecological dynamics to social systems (Levin et al., 2013). Management decisions that influence ES are often driven by expectations of multiple stakeholders and multiple management agencies that collectively define socio-political contexts (i.e. Fig. 2). These decisions can also engage scientists from several disciplines including sociologists, economists, geologists, and ecologists (Schröter et al., 2014). A key theme in the study of ESs, therefore, is the identification of holistic approaches that provide decision support for joint ways of thinking. Network approaches provide practical tools needed to examine factors that influence system stability (Levin et al., 2013) and can be used to make quantitative predictions that test a range of possible scenarios, reflecting socio-economic, political, and ecological interests (Marcot et al., 2006; McCann et al., 2006; Schmitt and Brugere, 2013). Ultimately, we expect that quantitative tools being used to combine BEF–FWT perspectives will support decision-making and assure broad-scale and long-term sustainability of resource use.

5. CONCLUSIONS

We conclude that network approaches are important tools that can be used to evaluate the contribution of diverse species assemblages to the maintenance of multiple EFs and ESs. The growth in network concepts over the last several decades, increasingly allows management decisions to be informed by more integrative approaches and evidence. In particular, our increased awareness of scaling, experimental replication of networks, and well-resolved webs that include multiple types of interactions are particularly valuable contributions to the understanding of the functions and services provided by diverse ecosystems. Although application still remains somewhat speculative, highly managed systems like agriculture (Macfadyen et al., 2011) and fisheries (Fung et al., 2015) currently provide the best examples of the potential for combined BEF and FWT approaches. Given the large-scale anthropogenic alteration of natural habitats (i.e. habitat destruction, biodiversity changes, nutrient pollution, and ocean acidification), we expect that understanding of species vulnerability and linkages developed in BEF experiments that adopt FWT approaches will provide valuable insights, which could be more broadly applied to the delivery, conservation, and restoration of ESs in the future.

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